

Definition, phylogenetic relationships and morphological species groups of taxon “*Macromischa*” (Hymenoptera: Formicidae: *Leptothorax*).

Definición, relaciones filogenéticas y grupos morfológicos de especies del taxon “Macromischa” (Hymenoptera: Formicidae: Leptothorax).

Jorge Luis Fontenla Rizo

Museo Nacional de Historia Natural, Obispo 61 esq. Oficinas, CP 10100. La Habana, Cuba.

Abstract

It is determined that arboreal and limestone-dweller species of Antillean *Leptothorax* conform a monophyletic group, named *Macromischa*, defined as the least inclusive clade that includes *L. sallei* and *L. myersi*, but not *L. isabellae*. The following morphological species groups are defined and diagnosed: Arboreal species: *sallei*, *squamifer* (subgroups *squamifer* and *splendens*), *gibbifer*, *purpuratus*, *punicans*. Limestone-dweller species: *versicolor* (subgroups *iris*, *porphyrytis*, *versicolor*). The Puerto Rican arboreal species, *L. isabellae*, is the *Macromischa*'s sister taxon. This more inclusive clade is named *Macromischamorpha*.

Resumen

Se determina que las especies arborícolas y carsifílicas de *Leptothorax* de las Antillas conforman un grupo monofilético, nombrado *Macromischa*, definido como el clado menos inclusivo que incluye *L. sallei* y *L. myersi*, pero no *L. isabellae*. Se definen y diagnostican los siguientes grupos morfológicos de especies. Arborícolas: *sallei*, *squamifer* (subgrupos *squamifer*, *splendens*), *gibbifer*, *purpuratus*, *punicans*. Carsifílicos: *versicolor* (subgrupos *iris*, *porphyrytis*, *versicolor*). La especie arborícola de Puerto Rico, *L. isabellae*, es el taxon hermano de *Macromischa*. Este clado más inclusivo es nombrado *Macromischamorpha*.

Key words: Ants, *Leptothorax*, *Macromischa*, phylogenetic analysis.

Palabras claves: Hormigas, *Leptothorax*, *Macromischa*, análisis filogenético.

INTRODUCTION

All of the Antillean *Leptothorax*, along with a group of species from Central America and the South of the United States, were placed in the genus ad hoc, *Macromischa* Roger, 1863, until BARONI-URBANI'S (1978) revision. He defined 12 species groups within the former *Macromischa* and treated it as a subgenus, with ambiguous limits and possibly polyphyletic, of *Leptothorax*. SNELLING (1986) synonymized formally the taxon, and this is the most accepted general consideration so far (BOLTON, 1994, 1995).

Within the Antillean *Leptothorax*, which conforms the richest group, both in species number and endemism, of all of the Antillean ants, it can be distinguished three general ecological species groups: **a)** terricolous: built their nests on soil. **b)** arboreal: built their nests in epiphytes, fallen trunks, holes in the trees or making a carton nest in the bran-

ches. c) limestone-dweller: built their nests in crevices of limestone, making a cartoon tubular entrance. This is an unique trait among ants.

The species in the arboreal and limestone-dweller groups exhibit a heterogeneous arrangement of traits like bizarre morphology and sculpturation and unusual color patterns. This, together with the singular nesting behavior of the limestone-dweller species, makes all of them one of the most remarkable group of ants in the whole world.

The purpose of the present paper is to define and to determine, through a phylogenetic analysis, a possible natural taxon as well as morphological species groups within the Antillean *Leptothorax*

MATERIAL AND METHODS

Taxa. There were analyzed the 47 species of Antillean *Leptothorax*. It was followed the taxonomic arrangement of BARONI-URBANI (1978), with later modifications and/or additions of SNELLING (1986) and FONTENLA (1997, 1998). It was not possible to examine specimens of *L. ciferrii*, *L. pulchellus*, *L. creolus* and *L. praecreolus*†. Characters selection and measurements of these species were taken from BARONI-URBANI (1978) for the extant taxa and from ANDRADE (1992) for the fossil species. The rest of the species were examined from the following collections: Cuba: Instituto de Ecología y Sistemática, Museo Nacional de Historia Natural. USA: American Museum of Natural History, Museum of Comparative Zoology at University of Harvard, National Museum of Natural History.

Characters. There were selected 52 morphological and one ecological-behavioural characters from workers (Appendix 1). Exclusive characters for particular species were not considered in the phylogenetic analysis (Appendix 3). Multistated characters were treated as unordered.

Polarization and outgroups. Polarization was made through an unconstrained and simultaneous analysis, as part of the cladistic performance. It was selected as prime outgroup *Cardiocondyla emeryi*. This genus is very close to *Leptothorax* (BOLTON, 1982; FRANCOEUR AND LOISELLE, 1988). *C. emeryi* is a widespread and very well known species with a conservative morphology. The second outgroup was *Leptothorax acervorum*, the type species of the genus, *sensu* BOLTON (1982, 1995).

Phylogenetic analysis. It was employed PAUP 3.1.1 program (SWOFFORD, 1993). Tree search was made by branch swapping together with tree bisection and reconnection. The choice of the final hypothesis of relationships was made after the application of successive weighting with the rescaled consistency index. Assumptions and comments of this method of reducing solutions in CARPENTER (1988, 1994) and EGGLETON AND VAN-WRIGHT (1994). Tree manipulation and edition with MacClade version 3.05 (MADDISON AND MADDISON, 1995).

Pylogenetic definitions. I follow here the approach to phylogenetic definitions sustained by SHANDER AND THOLLESSON (1995), MICHAEL (1995, 1998) and DOMINGUEZ AND WHEELER (1997), instead of the traditional approach (DE QUEIROZ, 1996, 1997 and references therein). They do not consider ancestry-descendant relationships as part of the phylogenetic definitions. For population level definition I follow DE QUEIROZ (1992).

RESULTS AND DISCUSSION

Cladistic analysis yielded 952 equally parsimonious trees (EPT) with Length (L)= 239 steps, Consistency Index (CI)= 0.28 and Retention Index (RI)= 0.78. After successive weighting, solutions were reduced to 2 EPT with CI= 0.52 and RI= 0.91. Strict consensus tree (Fig. 1) shows a clade (*) whose species share the following characters states: 24(0), 33 (1,2), 34(1), 35(1), 3(1), 53 (1,2). This clade includes all of the original species of *Macromischa*. *L. isabellae* is its sister group, sharing characters states 24(0), 34(1), 53(1). *L. praecreolus*† is the sister taxon of this more inclusive clade, sharing character state 34(1), and probable 53(1), according to the most probable parsimonious reconstruction. The *terricolous* species conform the BARONI-URBANIS'S (1978) *allardycei*, *creolus*, *pastinifer* and *pulchellus* morpho-logical groups. The *pulchellus* group appears to be polyphyletic (Composition of Baroni-Urbani's 1978 groups in Appendix 2).

In an attempt to refine the phylogenetic relationships of the arboreal + limestone dweller clade, it was removed the *terricolous* group and added to the root its sister species. The characters states were properly recodified when needed. The new performance produced 166 EPT with L= 183, CI= 0.35 and RI=0.74 . Successive weighting resulted in one tree (Fig. 2); with CI=0.61 and RI= 0. 88. Manipulation with MacClade did not reveal any shorter alternative tree topology.

Bootstrap majority-rule consensus tree (Fig. 3) shows support above 50% for all the branches. Generation of 10 000 random trees from the data matrix produced a tree frequency between 363 and 480 steps, with a mean value of 433.1 steps. This indicates that the most parsimonious reconstruction (183 steps) is very far from a chance solution and so the data contain a strong phylogenetic signal.

The arboreal + limestone dweller clade of Antillean *Leptothorax* can be named *Macromischa*. The meaning of this name is to point to a natural (monophyletic) group of species within the genus *Leptothorax*, which has evolved in a very specific biogeographical context: Cuba and the Hispaniola, producing two ecological and morphological well defined species groups. *Macromischa* can be defined (stem-based) as: the least inclusive clade that includes *L. sallei* and *L. myersi*, but not *L. isabellae*. The more inclusive clade composed by *Macromischa* and its sister taxon, *L. isabellae*, can be named as *Macromischamorpha* and defined (node-based) as: the least inclusive clade that includes *L. isabellae* and *Macromischa*. Morphological species groups of *Macromischa* (named according to nomenclatural priority).

1. *Sallei*. Definition: The least inclusive clade of *Macromischa* that includes *L. sallei* and *L. laetus*. Composition: *L. bruneri*, *L. dissimilis*, *L. laetus*, *L. hispaniolae*, *L. sallei*. Diagnosis: Arboreal species of medium size, slender constitution and straight profile. Club differentiated, scapes thin and short. Propodeal spines long. Petiole long, node square and high. Postpetiole broader than long. Femora medium. Femorae and tibiae inflated. Tegumentary sculpturation mainly longitudinal.

BARONI-URBANI (1978) included within his *sallei* group six species from Mexico and Central America. Cladistic analysis produced 40 EPT with L= 255, CI=0.26, and RI= 0.69. Successive weighting gave a single tree (CI= 0.40, RI= 0.80), which shows these spe-

cies as not belonging to *Macromischa* (Fig. 4).

2. *Squamifer*. Definition : The least inclusive clade of *Macromischa* that includes *L. squamifer* and *L. splendens*. Composition: *Squamifer* subgroup: *L. platynemis*, *L. barbouri*, *L. creighthoni*, *L. squamifer*. *Splendens* subgroup: *L. violaceus*, *L. splendens*, *L. darlingtoni*, *L. abeli*. Diagnosis: Arboreal species of big and medium size. Curvilinear or straight profile. Scapes thick and short. Propodeal spines present. Node scale shaped, high and broader than long. Postpetiole broader than long. Femora medium. Femorae and tibiae inflated. Tegument with iridescent or metallic reflections. *Squamifer* subgroup. Spines long. Petiole long or very long; node broader than the postpetiole. *Splendens* subgroup. Pronotum and mesonotum broad. Propodeal spines and petiole short. Femora with small tubercles.

3. *Gibbifer*. Definition: Types specimens of *L. gibbifer* Baroni-Urbani, 1978 and all other organisms relationed to those organisms through interbreeding to form an inclusive population level lineage. Composition: *L. gibbifer*. Diagnosis: Arboreal species of small size. Massive constitution and curvilinear profile. Club differentiated; scapes thick and short. Propodeal spines short. Petiole short; node rounded and high, with no anterior face and broader than long. Postpetiole broader than long. Femora medium. Femora and tibiae inflated. Tegument with iridescence. Reticulated sculpturation.

4. *Purpuratus*. Definition: The least inclusive clade that includes *L. alayoi* and *L. purpuratus*. Composition: *L. alayoi* and *L. purpuratus*. Diagnosis: Arboreal species of slender constitution. Club differentiated; scapes thick and short. Propodeal spines present. Petiole very long. Node rounded and very low, with no anterior face, longer than broad. Postpetiole longer than broad. Femora and tibiae inflated. Head with iridescent tegument.

5. *Punicans*. Definition: Types specimens of *L. punicans* Roger, 1863 and all the other organisms relationed to those organisms through interbreeding to form an inclusive population level lineage. Composition: *L. punicans*. Diagnosis: Arboreal species of big size and sinuous profile. Club differentiated; scapes thick and short. Propodeal spines absent. Petiole long, node rounded, low with no anterior face, longer than broad. Tibiae no inflated. Postpetiole longer than broad. Mesosoma punctuated and longitudinal striated.

6. *Versicolor*. Definition: The least inclusive clade of *Macromischa* that includes *L. iris*, *L. porphyrytis* and *L. versicolor*. Composition: *Iris* subgroup: *L. gundlachi*, *L. wheeleri*, *L. barroi*, *L. iris*, *L. senectutis*. *Porphyrytis* subgroup: *L. mortoni*, *L. nipensis*, *L. villarensis*, *L. banao*, *L. myersi*. *Versicolor* subgroup: *L. versicolor*, *L. bermudezi*, *L. poeyi*. Diagnosis: Slender constitution, club poorly differentiated, scapes thin and long or very long. Petiole long or very long; node rounded, longer than broad. Postpetiole longer than broad (except in *L. myersi*). Tibiae no inflated. *Iris* subgroup: scapes surpassing CL in less than 140%. Propodeal spines absent. Petiole long. Femora medium. Tegument with iridescent and/or metallic reflections. *Porphyrytis* subgroup: scapes surpassing CL in less than 140%. Propodeal spines long or very long. Petiole long or very long. Femora long. *Versicolor* subgroup: Scapes surpassing CL in more than 140%. Pronotum oblong. Propodeal spines absent. Petiole long. Femora long.

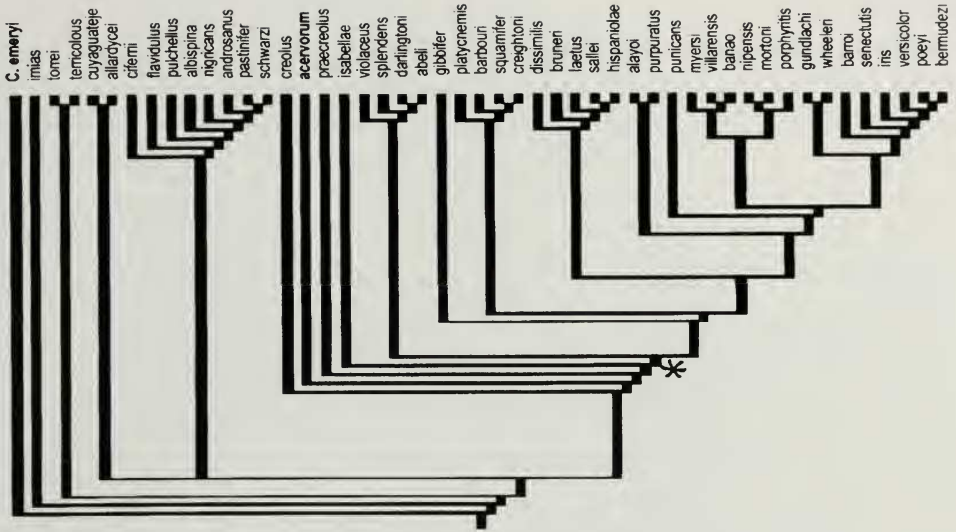


Figure 1. Strict consensus tree of the phylogenetic relationships of Antillean *Leptothorax*. Consistency Index= 0.52, Retention Index= 0.91. Species in bold characters: outgroups.

Figura 1. Árbol de consenso estricto de las relaciones filogenéticas de *Leptothorax* antillanos. Índice de Consistencia= 0.52, Índice de Retención= 0.91. Species in bold characters: outgroups.

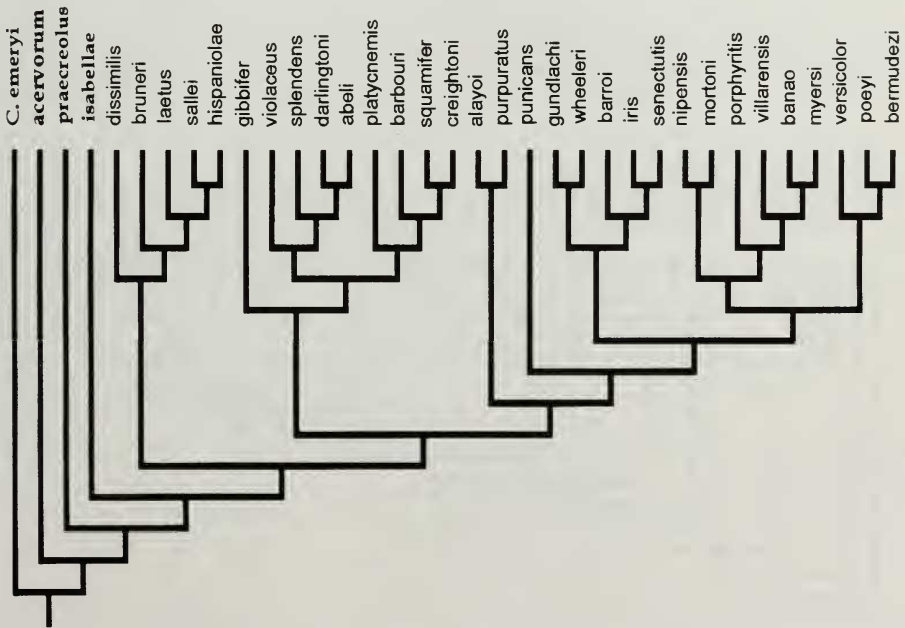


Figure 2. Phylogenetic relationships of phylogenetic taxon *Macromischa*. Consistency Index= 0.60, Retention Index= 0.88. Species in bold characters: outgroups.

Figura 2. Relaciones filogenéticas del taxon filogenético *Macromischa*. Índice de Consistencia= 0.60, Índice de Retención= 0.88. Species in bold characters: outgroups.

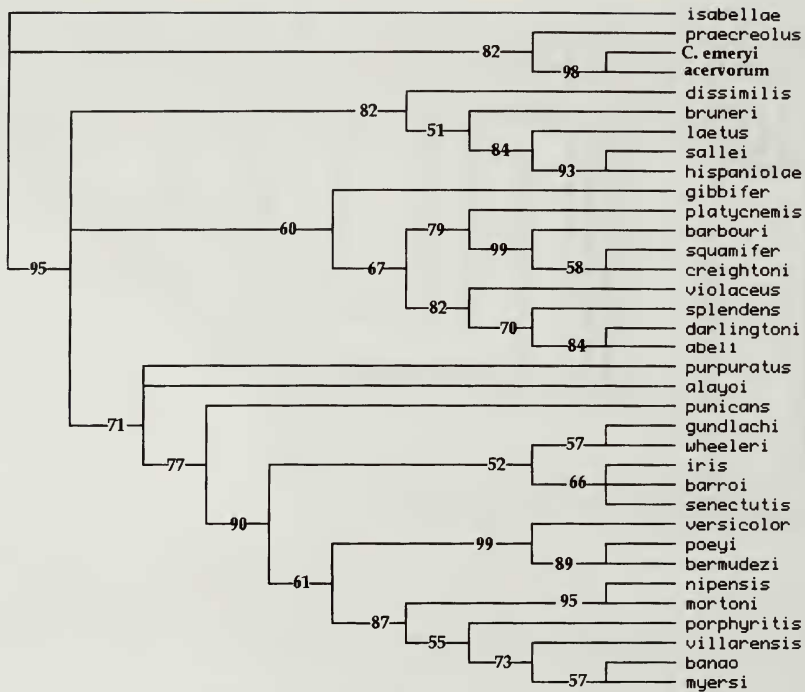


Figure 3. Bootstrap majority-rule consensus tree of *Macromischa*.
Figura 3. Árbol de consenso de la mayoría de análisis de Bootstrap de *Macromischa*.
Species in bold characters: outgroups.

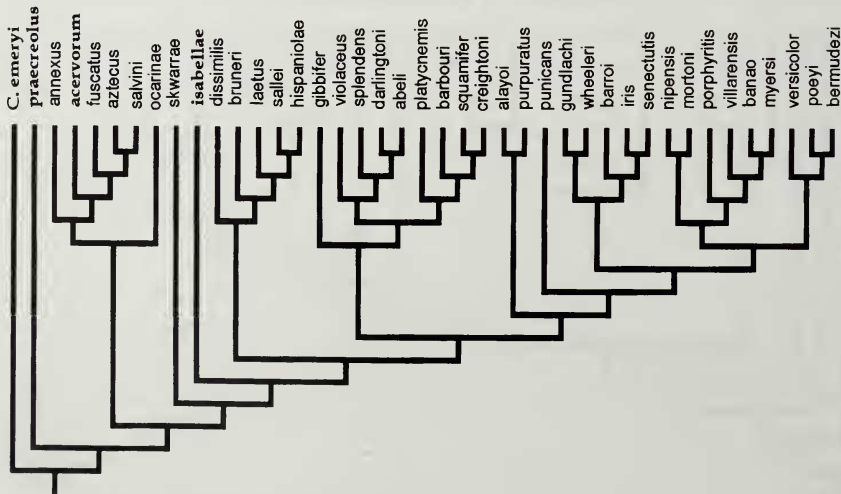


Figure 4. Cladistic relationships among continental species of BARONI-URBANIS's (1978) *sallei* group and *Macromischa*. Consistency Index= 0.40, Retention Index= 0.80.
Figura 4. Relaciones cladísticas entre las especies continentales del grupo *sallei*, sensu BARONI-URBANI (1978) y *Macromischa*. Índice de Consistencia= 0.40, Índice de Retención= 0.80.
Species in bold characters: outgroups.

ACKNOWLEDGMENTS

My gratefulness to Rare Center for Tropical Conservation of Philadelphia, USA, for the financial support. To Drs. E. O. Wilson and D. Smith for the loan of specimens and other facilities, and also to S. Cover. To my colleagues at the MNHNC for their criticisms.

BIBLIOGRAPHY

- ANDRADE, M.L. 1992. First fossil "true *Macromischa*" in amber from the Dominican Republic (Hymenoptera: Formicidae). *Mitteil. Schweiz. Ent. Gesell.*, 65:341-351.
- BARONI-URBANI, C. 1978. Materiali per una revisione dei *Leptothorax* Neotropici appartenente al sottogenere *Macromischa* Roger, n. comb. (Hymenoptera: Formicidae). *Entomol. Basil.*, 3:395-618.
- BOLTON, B. 1982. Afrotropical species of the myrmicinae ant genera *Cardiocondyla*, *Leptothorax*, *Melissotarsus*, *Messor* and *Catalaucus* (Formicidae). *Bull. British Mus (Nat. Hist.)*, 45:307-370.
- BOLTON, B. 1994. *Identification guide to the ant genera of the world*. Harvard University Press. Cambridge, Massachusetts, 222 pp.
- BOLTON, B. 1995 *A new general catalogue of the ants of the world*. Harvard University Press. Cambridge, Massachusetts, 504 pp.
- CARPENTER, J.M. 1988. Choosing among multiple equally parsimonious cladograms. *Cladistics*, 4:291-296.
- CARPENTER, J.M. 1994. Successive weighting, reliability and evidence. *Cladistics*, 10:215-220.
- DE QUEIROZ, K. 1992. Phylogenetic definition and taxonomic philosophy. *Biol. Philos.*, 7:295-313.
- DE QUEIROZ, K. 1996. A phylogenetic approach to biological nomenclature as an alternative to the Linnean systems in current use. In J.L. Reveal (ed.). *Proceedings of a mini-symposium on biological nomenclature in the 21st century*. University of Maryland: www.life.umd.edu/bees/96sym.html.
- DE QUEIROZ, K. 1997. The Linnean hierarchy and the evolutionization of taxonomy, with emphasis on the problem of nomenclature. *Aliso*, 15: 125-144.
- DOMINGUEZ, E., AND Q.D. WHEELER. 1997. Taxonomic stability is ignorance. *Cladistics*, 13: 367-372.
- EGGLETON, P., AND R.I. VANE-WRIGHT. 1994. *Some principles of phylogenetics and their implications for comparative biology*. In: P. Eggleton R.I. Van-Wright. (eds) Academic Press London. Phylogenetics and ecology. pp:345-367.
- FONTENLA, J.L. 1997. Notas y sinónimos nuevos de *Leptothorax* (Hymenoptera: Formicidae) de Cuba. *Avicennia*, 6/7: 47-53.
- FONTENLA, J.L. 1998. New species of *Leptothorax* (Hymenoptera: Formicidae) from Cuba. *Avicennia*, 6/7: 47-53.
- FRANCOEUR, A., AND R. LOISELLE. 1988. *The male of Leptothorax with notes on the subgenus Nesomyrmex*. (Formicidae: Hymenoptera). In: J.C. Trager. (ed) University of Cornell, Ithaca, New York. Advances in myrmecology. pp:43-54.
- MADDISON W.P., Y D.R. MADDISON. 1992. *Mac Clade: Analysis of phylogeny and character evolution*. Version 3. Sunderland/Mass. (Sinauer Associates), 245 p.
- MICHAEL, S.Y. LEE. 1996. The phylogenetic approach to biological taxonomy: practical aspects. *Zool. Scr.*, 187-190.
- MICHAEL, S.Y. LEE. 1998. Ancestor and taxonomy. *TREE*, 13: 109.
- ROGER, J. 1863. Die neu aufgeführten Gattungen und Arten meines Formicidae verzeichnisses, Nebs Ergänzungen einiger früher gegeben Beschreibungen. *Berl. Ent. Zeitschr.*, 7:131-214.
- SCHANDER, C., AND M. THOLLESSON. 1995. Phylogenetic taxonomy- some comments. *Zool. Scr.*, 24: 263-268.
- SWOFFORD, D.L. 1993. *PAUP: Phylogenetic analysis using parsimony, version 3.1.1. Computer program and user manual*. Distributed by the Illinois Natural History Survey, Champaign, Illinois.
- SNELLING, R.R. 1986. New synonymy in Caribbean ants of the genus *Leptothorax* (Hymenoptera: Formicidae). *Proc. Entomol. Soc. Wash.*, 88:154-156.
- WILSON, E.O. 1988. In: J. Liebherr (ed.) *Zoogeography of the Caribbean insects*. Cornell University Press. Ithaca, New York. The biogeography of the West Indian ants (Hymenoptera; Formicidae). pp:214-230.

Appendix 1. Characters and codification.

Apéndice 1. *Caracteres y codificación.*

1. CW/CL $\leq 75\%$ (0), CW/CL $\geq 75\%$ (1). CW: Cephalic width. CL: Cephalic length.
2. Antennal club: little differentiated (0), well differentiated (1).
3. Number of segments in the club: 3 (0), 4 (1).
4. Shape of funiculum segments: rounded (0), rectangular (1).
5. Scape: thick (0), thin (1).
6. Scape: short (0), long (1), very long (2).
Short: do not surpass CL, long: surpassing CL less than 140%, very long: surpassing more than 140%.
7. Size: small (0), medium (1), big (2).
Small ≤ 35 mm, medium > 3.5 mm < 5.0 mm, big ≥ 5.0 mm.
8. Profile : straight (0), curvilinear (1), convex (2), sinuous (3).
9. Pronotum shape in profile: no oblong (0), oblong (1).
10. General body structure: massive (0), slender (1).
11. Pronotum width /Mesosoma length : broad $\geq 50\%$ (0), narrow $\leq 50\%$ (1).
12. Mesonotum width/Pronotum width: Broad $\geq 85\%$ (0), narrow $\leq 85\%$ (1).
13. Metanotum width/ mesonotum width: > 100 (0), < 100 (1).
14. Metanotum width/pronotum width $\geq 75\%$ (0), $\leq 75\%$ (1).
15. Petiole length, measured as petiole length /mesosoma length ratio: short ($<45\%$) (0), long ($>45\%$ $<50\%$) (1), very long ($> 50\%$) (2).
16. Petiole node height, measured as petiole node height (PH)/petiole length (PL) ratio: low ($< 40\%$) (0), high ($\geq 40\%$, $\leq 50\%$) (1), ($>50\%$) (2).
17. Petiole node width (PW)/petiole length (PL): narrow ($\leq 45\%$) (0), broad ($> 45\%$) (1).
18. Petiole node: taller than broad (0), broader than tall (1).
19. Petiole node: broader than long (0), longer than broad (1).
20. Petiole node: less broad than postpetiole (0), broader than postpetiole (1).
21. Petiole node without an anterior defined face (0), with an anterior defined face (1).
22. Petiole node shape in profile: square or subsquare (0), rounded (1), scale (2), anterior face concave (3).
23. Postpetiole: narrow (0), broad (1), very broad (2). Narrow: longer than broad; broad: postpetiole width (PPW)/ postpetiole length (PPL) $<150\%$; very broad: PPW/PPL $> 150\%$.
24. First segment of gaster: narrower than pronotum width (0), broader than pronotum width (1).
25. Subpetiolar process: absent (0), present (1).
26. Petiole peduncle: with no hair or very scarce hair (0), hair abundant (1).
27. Propodeal spines: absent (0), short (1), long (2). Length measured as spine length (SL) /mesosoma length (ML) ratio: short: SL/ML $\leq 30\%$, long. SL/ML $> 30\%$.
28. Maximal /minimal posterior femur width ratio: little contrasting $> 30\%$ (0), contrasting $\leq 30\%$.
29. Femora thickness: little marked (0), well marked (1).
30. Distribution of femora thickness: homogeneous throughout (0), medial (1), distal (2).
31. Femorae tubercles: absent (0), present (1).

32. Tibiae: no inflated (0), inflated (1).
33. Posterior femorae: short (0), medium (1), long (2). Short: length $\leq 70\%$ mesosoma length (ML), medium $70\% < ML \leq 100\%$, long: $> 100\% ML$.
34. Promesothoracic suture: no conspicuous or absent (0), conspicuous (1).
35. Dominant pilosity: hairs short and blunt (0), hairs long and acuminate (1).
36. General pilosity distribution: scarce (0), abundant (1).
37. Scape: With no erect hairs (0), with erect hairs (1).
38. Head: striae absent or feeble and sparsely (0), striae strong and dense (1).
39. Head: punctures absent or feeble and sparse (0), punctures marked and dense (1).
40. Mesosoma: striae absent or feeble and sparsely (0), striae strong and dense (1).
41. Mesosoma: punctures absent or feeble and sparsely (0), striae strong and dense (1).
42. Pronotum: sculptured like the rest of mesosoma (0), sculpturation absent or very feeble (1).
43. Petiole: not striated (0), striated (1).
44. Petiole: not punctuated (0), punctuated (1).
45. Postpetiole: not striated (0), striated (1).
46. Postpetiole: not punctuated (0), punctuated (1).
47. Legs: with no microsculpturations (0), with sculpturations (1).
48. Tegumentary iridescent: absent (0), present (1).
49. Tegument with metallic reflections: absent (0), present (1).
50. Tegument: no polychrome (0), polychrome (1).
51. Gaster: with no microsculpturations (0), with microsculpturations (1).
52. Gaster: shining or slightly shining (0), opaque (1).
53. Nesting behaviour: terricolous (0), arboreal (1), limestone (2).

Appendix 2. Composition of BARONI-URBANI'S (1978) morphological species groups of subgenus *Macromischa* of Antillean *Leptothorax*. Species in synonymy or with nomenclatorial changes. * (SNELLING, 1986), ** (FONTENLA, 1997).

Apéndice 2. Composición de los grupos morfológicos de especies del sugénero *Macromischa* de *Leptothorax* antillanos, según BARONI-URBANI (1978). Especies en sinonimia o con cambios nomenclatoriales. *SNELLING (1986), **FONTENLA (1997).

1. *allardycei*: *L. allardycei*. 2. *creolus*: *L. creolus*. 3. *gibbifer*: *L. gibbifer*. 4. *gundlachi*: *L. aguayoi* (= *L. gundlachi***), *L. gundlachi*, *L. senectutis*, *L. wheeleri*. 5. *isabellae*: *L. isabellae*, *L. hyperisabellae* (= *L. isabellae**), *L. muticus* (= *L. isabellae**). 6. *pastinifer*: *L. pastinifer*, *L. pastoris* (= *L. pastinifer***), *L. schwarzi*. 7. *pulchellus*: *L. albispina*, *L. androsanus*, *L. ciferrii*, *L. flavidulus*, *L. pulchellus*, *L. terricolous*, *L. torrei*. 8. *punicans*: *L. punicans*. 9. *purpuratus*: *L. alayoi*, *L. mortoni*, *L. myersi*, *L. porphyritis*, *L. purpuratus*, *L. williamsi* (= *L. villarensis**). 10. *Sallei**: *L. bruneri*, *L. dissimilis*, *L. hispaniolae*, *L. sallei*, *L. similis* (= *L. laetus**), *L. umbratipes* (= *L. laetus***). 11. *squamifer*: *L. barbouri*, *L. creightoni*, *L. darlingtoni*, *L. opalinus* (= *L. darlingtoni***), *L. platycnemis*, *L. scabripes* (= *L. splendens***), *L. splendens*, *L. squamifer*, *L. violaceus*. 12. *versicolor*: *L. anemicus* (= *L. bermudezi***), *L. bermudezi*, *L. iris*, *L. poeyi*, *L. rugiceps* (= *L. poeyi*), *L. versicolor*.

* continental *sallei*: *annexus*, *aztecus*, *fuscatus*, *ocarinae*, *salvini*, *skwarrae*.

Apendix 3. Character codification in Antillean *Leptothorax*.

Outgroups in bold characters.

Apéndice 3. Codificación de caracteres en *Leptothorax* de las Antillas.

Grupos externos en negrita.

	123456789012345678901234567890123456789012345678901234567890123
C. emeryi	11001003000000021000001100100000000000101001110000000
acervorum	1100000000100102200010101011010000000101001010000000
poeyi	00011220110000100010010001001200211100010000000000002
bermudezi	00011220110000100010010001001200211100111000000000002
versicolor	00011220110000100010010001001100211100111010001000112
iris	0001111010000110010010001001100111100110010000100002
barroi	0001121101001011001001001100110011110010010000100002
senectutis	00011111010010110010010011001100111100010010000100002
gundlachi	10011111010010110010010011001100111110110010000010002
wheeleri	10011110010010110010010011001100111110010010000010002
punicans	11000023010010100010110011011100111111011001010000001
purpuratus	11000020010000200010010011201101111111010000000100001
alayoi	110010110100002000100100110110111111010000000100001
villarensis	11111120010010200010110011210100211111010011000000002
banao	10111120010011200010010011210100211111010010100000002
porphyritis	1001112001001020001011001121010021111111011110000002
nipensis	1001112001001110001001001121010021111111011111000112
mortoni	10011120010011100010010011210100211111101011010000112
myersi	10111120010011110010111011210100211110110010000000002
squamifer	110000200000112110112101120110111110010000000110001
creightoni	1100002000001121101121011201101111111010000000110001
barbouri	1100002000001121101121011201101111111010000000100001
darlingtoni	1100002100110101100012100110111111111010100000101001
splendens	1100001100110101100012101101111111111010000000101001
abeli	11000011001101011000121001101111111110010100000101001
violaceus	1100001100110101100012100110111111111000000000100001
platycnemis	110000210001012100011200112011011111111010000000100001
gibbifer	11000001001000001000010011001101111111010010010100001
sallei	11011010010011110000101001211101111111010010100000001
hispaniolae	11011010010011110000101000211101111111010010000000001
laetus	1101101001001021000000100120110111111110010100000001
bruneri	1101101001000011000000100110110111111110011100000001
dissimilis	1101101001000011000000100110110111111110001010000001
isabellae	11010011011000011000011010101100110001111001011000001
praeceolus	1100001001000001100000101110110001000010100110000000?
pastinifer	11001101001101021100131111210000200001111001011000000
schwarzi	1100100200110102110113211111100000000000000000000000
androsanus	110010010011010211001021111110000000011100111000000
torrei	110000010000000110001111011100000000101001010000000
terricola	1100000100000001100011110111000100000001001000000000
nigricans	11001002000000011100102111211000000000101001011000000
albispina	1100000100100002110010211011100000000010100101000000
flavidulus	1100000100100002100010211011100000000000100100000000
cuyaguaje	1100000200100002100012111111100000000010100001000000
pulchellus	110000010010000211001021101110000000000000000000000
ciferrii	110000010010000100001021101110000000001000101000000
creolus	1100000100100001100010101011100000000010100101000000
allardycei	1100000100110001110010111011100000000101001010000000
imias	11000001000000011000002110111000000000111001010000000